First record and a description of a new species of *Oregodasys* (Gastrotricha: Macrodasyida: Thaumastodermatidae) from Tobago

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Abstract.—A new species of Oregodasys (Gastrotricha: Macrodasyida: Thaumastodermatidae) is described from sublittoral sediments on the island of Tobago. Oregodasys ashleigha sp. nov. is 430–465 μ m long and characterized by the presence of a pair of large and elliptical red ocelli, numerous cirri (21–23) restricted to the posterior end, and an inflated, bilobed caudum. Adhesive tubes are present in four series as TbA (10/side), TbL (10/side), TbVL (up to 45/side), and TbP (up to 51 total). The structure of the reproductive system is characteristic of the genus and defined by posterior ovaries, a single right testis, a bipartite caudal organ complex, and a frontal organ. The bipartite caudal organ complex is distinctly muscular, with the right-side caudal organ wrapped in spiral muscles and the left-center side caudal organ wrapped in circular muscles.

Keywords: meiofauna, Gastrotricha, Macrodasyida, Caribbean, confocal, new species, *Oregodasys ashleigha*

Gastrotrichs are abundant and diverse meiofaunal invertebrates that have been described from marine and freshwater sediments across the globe. Gastrotricha is divided into two orders, Chaetonotida and Macrodasyida, based on general body shape, the presence and distribution of adhesive tubes, their reproductive anatomy, and the structure of the myoepithelial pharynx. The Thaumastodematidae is the largest family of macrodasyidan gastrotrichs with more than 165 marine species distributed across eight genera (Hummon & Todaro 2010, Todaro et al 2011). Species of Oregodasys are common in intertidal and subtidal sediments and easily distinguished from other species of Thaumastodermatidae by their scale-less cuticle (also in most species of *Ptychostomella*) that is nevertheless adorned with numerous papillae and abundant epidermal glands (Todaro & Hummon 2008). To date, species of Oregodasys have been described from the coasts of Europe (Remane 1927, Swedmark 1956, Forneris 1961, Boaden 1965, Clausen 1965, Hummon 2008, Rothe & Schmidt-Rhaesa 2010), the Galapagos (Schmidt 1974), Japan (Chang et al. 2002) as well as several islands in the Caribbean (Hochberg 2010, Hochberg et al. 2014). Among the 15 described species, five species present the relatively uncommon morphological condition of possessing pigmented ocelli, which are appear red under reflected light: O. ruber (Swedmark, 1956), O. tentaculatus (Swedmark, 1956), O. styliferus (Boaden, 1965), O. ocellatus (Clausen, 1965) and O. norenburgi Hochberg, 2010. On a recent trip to the island of Tobago (Republic of

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DOI: 10.2988/0006-324X-128.3.176

Trinidad and Tobago), we discovered a sixth species of *Oregodasys* with red ocelli that we describe herein.

Materials and Methods

Samples of marine meiofauna were collected on the island of Tobago. A Memorandum of Understanding with the Institute of Marine Affairs in Trinidad was obtained in 2012 prior to sampling for meiofauna. Samples of sediment were collected by SCUBA on 31 July 2012 at 88 m depth at a location $(11^{\circ}18'0.086''N,$ 060°31'0.236"W) west of Goat Island on the northeast side of Tobago. Water temperature was recorded at the dive site and sand was collected for granulometric analysis. Sediments were placed in plastic bags and brought back to the Manta Lodge in Speyside, Tobago for analysis in make-shift labs.

Meiofauna was extracted from the sediment with isotonic MgCl₂ using the anesthetization-decantation technique (Pfannkuche & Thiel 1988) in 1L plastic Erlenmeyer flasks. Animals were decanted onto 35 µm sieves and washed with natural seawater into Petri dishes. Meiofauna were observed with Leica EZ4 stereomicroscopes and then transferred to glass slides for specific identification on a Zeiss A1 compound microscope equipped with DIC and Sony Handycam digital video cameras. All gastrotrichs were measured with an ocular micrometer. The position of anatomical characters is provided in percent units (U) of total body length (anterior tip of body (excluding cilia) = U00, posterior tip of body = U100).

Several gastrotrichs were fixed in 2.5% glutaraldehyde in 0.1M cacodylate buffer (pH 7.4) for making permanent slides after returning to the University of Massachusetts Lowell. Gastrotrichs were rinsed in PBS for 1 hr and dehydrated in ethanol (70%, 90%, 100%, 100% x 10 min each) prior to transfer to propylene oxide (2×15

min) and followed by embedment in epon resin on glass slides. Four specimens are archived at the Smithsonian Institution, Washington, D.C., USA.

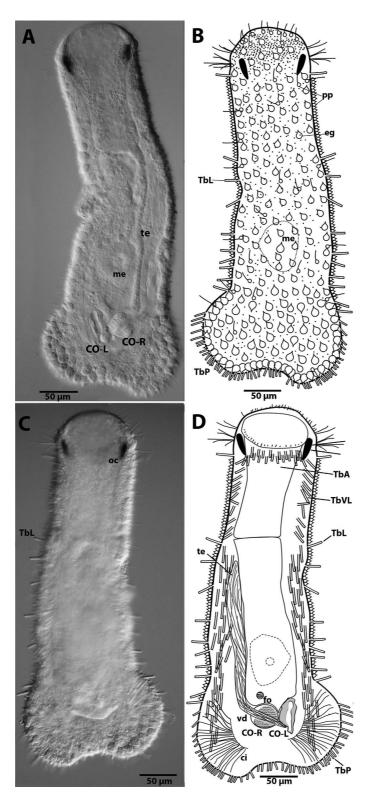
Additional specimens (N = 2) were fixed in 4% paraformaldehyde in 0.1 M phosphate buffer saline (pH 7.2) for at least one week. Specimens were then rinsed in PBS and stained in Alexa Fluor 488 phalloidin (Life Technologies) to document the musculature. Stained specimens were briefly rinsed in PBS before mouting in Fluoromount G (Southern Biotechnology Associates, Birmingham, AL) on glass slides. An Olympus FV 300 confocal laser-scanning microscope was used to visualize the specimens. An argon laser (488 nm) was used to excite the samples, and Olympus software was used to capture the images. Confocal z-stacks were collected and processed in as .TIF files and .MOV video files. Files were further processed with Volocity (Perkin Elmer) to generate z-projections.

Sediments collected from the dive site were brought back to the University of Massachusetts Lowell and analyzed for granulometry. Sediments were dried in an oven at 100°C for 24 h and then sorted on Gilson SS-15 sieve shaker with mesh sizes of 2mm, 1mm, and 500, 250, 125, and 63 μ m. Sediment fractions were weighed and granulometric characters (median, st. dev., skeweness, kurtosis, median) were calculated using GRANPLOTS with line segments (Balsillie et al. 2002).

Abbreviations: BL, total body length; CO-R, right-side caudal organ; CO-L, leftside caudal organ; PhIJ, pharyngeointestinal junction; TbA, anterior adhesive tubes; TbL, lateral adhesive tubes; TbP, posterior adhesive tubes; TbVL, ventrolateral adhesive tubes.

Taxonomic Account

Order Macrodasyida Remane, 1925 [Rao and Clausen, 1970] Family Thaumastodermatidae Remane, 1927 Subfamily Thaumastodermatinae



Remane, 1927 Genus Oregodasys Hummon, 2008 Oregodasys ashleigha, new species Figs. 1–3

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Material examined.—Holotype in resin, USNM 1283149. Three paratypes in resin, USNM 1283150, USNM 1283151, and USNM 1283152. ZooBank access: http:// zoobank.org/urn:lsid:zoobank.org:pub: D7E5E456-2D2B-426B-88A7-1B93A54F 3129

Type locality.—Bare sand, 88 m depth. Temperature, 28°C; sediment characteristics: mean, 1.7498 phi; SD, 0.8278; skewness, 0.9777; kurtosis, 3.1332; median, -1.066.

Etymology.—The species is named in honor of Dr. Ashleigh Smythe, who cheerfully assisted with the collections and the research on Tobago.

Diagnosis.—Body length of 435–490 µm (mean 467.5 μ m, n = 10). Maximum body width at mouth, neck, U50 and caudal end of body is 77.5/107.5/125/185 µm, respectively. Pharynx length 127.5-142 µm (measured from the tip of the oral hood); oral hood to 37.5-47µm long; mouth to 72-77.5 µm wide. Two red ocelli total; one present on either side of mouth at the lateral margins, 25-32.5 µm long. Cuticle is translucent and covered with ciliated papillae on dorsal and lateral surfaces. Numerous epidermal glands fill the dorsal and lateral epidermis. A row of 10 TbA insert directly on the body surface and lead imperceptibly to the adhesive tubes of the TbVL series. TbVL elongate, up to 45 per side. TbL shorter than TbVL, 10 per side, beginning at U14 extending to U77. Caudal end inflated and bilobed, somewhat heart-shaped, with 51 TbP present on periperhy of inflated region. Locomotory cilia form transverse rows on the ventral surface from mouth margin to caudum. Approximately 21–23 ventral caudal cirri per side, to 48 μ m long, present beginning ca. U85. Hermaphroditic, with paired posterior ovaries and a single testis on left side as seen from the ventral side; egg dorsal at mid-body length; bipartite caudal organ with an oval musculoglandular portion on the right side and a spindleshaped portion on the center-left side; frontal organ present.

Description.-We investigated 10 specimens and the type description is based on an adult specimen of 465 µm (435–490 µm) total body length (Fig.1). One elliptical red ocellus is present on either side of the mouth margin, approximately 25 µm (25-32.5 µm) in length. Papillated oral hood to 42.5 μ m (37.5–47 μ m) long from mouth margin to tip of hood; scattered sensory cilia along hood to 6 µm long. Pharynx is 142.5 µm (127.5-142 µm) in length from tip of oral hood to PhIJ. Caudal end made of two rounded lobes, somewhat heartshaped (Figs. 1A-D, 2C). Body width at mouth, neck, U50, and caudal end is 77.5/ 107.5/125/185 µm, respectively.

Body covering of triangular-shaped papillae to 10 μ m long (Fig. 2C inset). Several papillae are closely associated with an apparent sensory cilium to 15–20 μ m long. The dorsal, lateral, and ventrolateral body surfaces are completely covered by papillae. Most papillae appear to be closely associated with an underlying epidermal gland of ca. 10 μ m diameter, although a precise connection between them could not be determined. Some papillae did however contain ovoid secretions, presumably from

Fig. 1. *Oregodasys ashleigha*. A, dorsal view of a live adult showing the general body shape and relevant characters. B, schematic drawing of dorsal view. C, ventral view of a live adult. D, schematic of ventral view. Abbreviations: ci, cirri; eg, epidermal glands; CO-R and CO-L, bipartite caudal organ complex; fo, frontal organ; me, mature egg; oc, ocellus; pp, papillae; TbA, anterior adhesive tubes; TbL, lateral adhesive tubes; TbP, posterior adhesive tubes; TbVL, ventrolateral adhesive tubes; te, testis; vd, vas deferens.

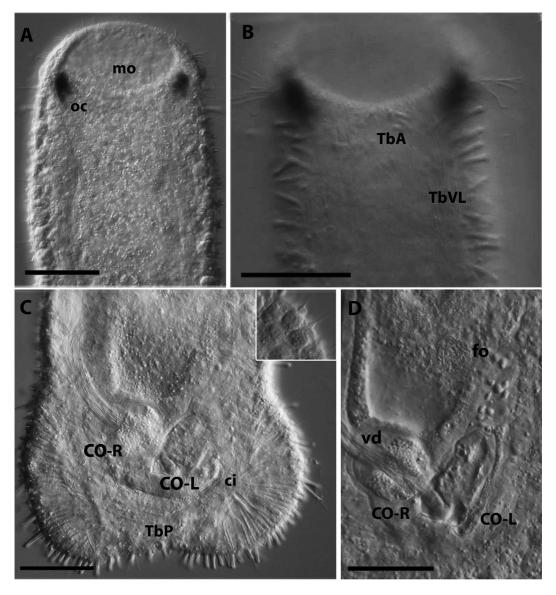


Fig. 2. *Oregodasys ashleigha*. A, dorsal view of head. B, ventral view of head. C, ventral view of caudal end. D, focus on reproductive organs at caudal end at ventral view. Inset: Closeup of papillae on dorsal side. Abbreviations: ci, cirri; CO-R and CO-L, bipartite caudal organ complex; fo, frontal organ; mo, mouth; TbA, anterior adhesive tubes; TbVL, ventrolateral adhesive tubes; TbP, posterior adhesive tubes.

the underlying glands. Most epidermal glands were translucent but completely filled the epidermis.

Adhesive tubes.—Adhesive tubes are present in four series (TbA, TbL, TbVL, and TbP) and showed no variability in number. Anterior adhesive tubes, 10 TbA per side, form a transverse row beneath the ventral mouth margin and are oriented toward the lateral body margin. All tubes insert directly on body surface, and are somewhat staggered in placement. Tubes range in size from 7–14 μ m long, with the most medial tubes the shortest and the lateral tubes the longest. The ventrolateral adhesive tubes (TbVL) are positioned on

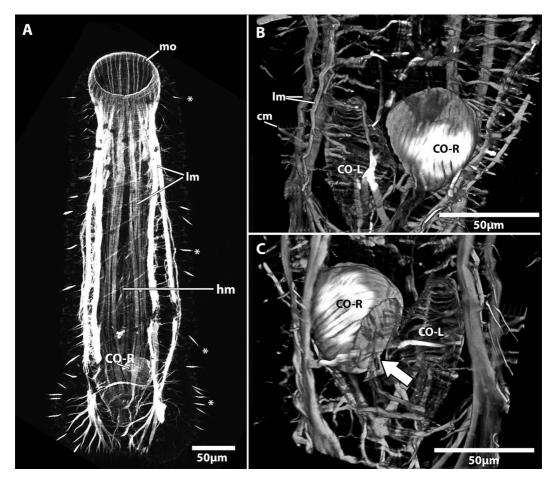


Fig. 3. *Oregodasys ashleigha*. A, confocal photomicrograph of a phalloidin-stained specimen showing the muscular system, ventral view. B, volocity-rendered view of the bipartite caudal organ complex as seen from the dorsal side. C, volocity-rendered view of the bipartite caudal organ complex as seen from the ventral side. Note the absence of muscles from the CO-R on its ventroposterior surface (arrowhead). Abbreviations: CO-R & CO-L, bipartite caudal organ complex; cm, circular muscles; hm, helicoidal muscles; mo, mouth; lm, longitudinal muscles; *, adhesive tubes with non-specific phalloidin staining.

either side of the ventral locomotory ciliary area and extend from approximately U12 to the caudal end. Anteriorly, the TbVL merge imperceptibly with the TbA, but are easily distinguished from them due to their arrangement in a mostly singular column. The TbVL in the pharyngeal region (U12–U28) are shorter (ca. 14 μ m minimum) than in the trunk where they are highly elongate (up to 23 μ m); numerous tubes insert in proximity to one another along the length of the column. All specimens had 45 tubes per side in the trunk region, U29 to the end body. A distinct set of 10 lateral adhesive tubes (TbL) per side, 15–16 μ m long, are distributed at U14/U37/U41/U48/U57/U61/U65/U70/U74/U77, respectively. The caudum is formed of two large, rounded lobes approximating a heart-shape and bearing 51 posterior adhesive tubes (TbP). TbP can be differentiated from TbL by their exclusive position on the inflated rounded caudum, beginning around U79. Tube length 10–11 μ m.

Cilia.—The ventral locomotory ciliature forms a continuous series of transverse rows from the ventral mouth margin to the posterior end. A transverse row of cilia is present posterior of the opening of the caudal organ/anus region around U89. All cilia are up to 15 μ m long.

Cirri.—Elongate cirri, 21–23 per side, are present in the posterior trunk region, beginning ca. U85, where the caudal end becomes inflated. The cirri insert slightly medial to the last TbVL along a region approximately 48 μ m long, forming a slight arc along this length. Each cirrus extends laterally up to 48 μ m long and was never observed to extend beyond the body wall (Figs 1D, 2C).

Digestive tract.—The digestive tract begins with a wide mouth with a mostly smooth margin, 77.5 μ m wide, covered by an oral hood. The mouth leads to the pharynx of similar width that narrows to ca. 42 μ m at the PhIJ (U31). The pharyngeal pores, which were observed in only one specimen due to the opacity of the body wall, are at ca. U26. Several specimens possessed numerous diatom frustules in their guts. The anus opens ventrally around U89.

Reproductive anatomy.—Simultaneous hermaphrodites. A single testis is present on the right side and close to the PhIJ; a vas deferens extends posteriorly to the caudal organ complex. The vas deferens passes into the muscular caudal organ complex on the right side of the body at the posterior end and appears to pass through CO-R and terminate in the region where CO-R and CO-L meet. The caudal organ is bipartite and consists of an oval glandulomuscular region (CO-R) slightly right to the median plane and a more spindle-shaped region (CO-L) that is oriented diagonally to it on the left to the median plane. CO-R is up to 41 µm (39-41 μ m, n = 2) long and 37 μ m (36–37 μ m, n = 2) wide and appears to contain numerous spherical secretions; CO-L is up to 58 µm $(57-58 \ \mu m, n = 2) \text{ long and } 24 \ \mu m (22-24)$

 μ m , n = 2) wide and both parts of the caudal organ complex (CO-R / CO-L) join with their posteriorly directed parts and it seems that their lumina communicate (Fig. 2D). A frontal organ (putative seminal receptacle) is present anterior to the CO-L around U75. A large mature oocyte (43 μ m long x 41 μ m wide) is dorsal to the gut in the mid-trunk region (Fig. 1A).

Musculature.—The musculature is present in circular, longitudinal and helicoidal orientations (Fig. 3A). Circular muscles and longitudinal muscles are present in somatic and splanchnic (gut) positions. We refrain from a full description of the somatic and splanchnic muscles, which will be presented in a more complete study at a later date. Instead, we focus only on the muscles of the reproductive system for comparison to O. cirratus, the only other species for which confocal data exists (Rothe & Schmidt-Rhaesa 2010). The Tobagan specimens' singular right testis is wrapped in circular muscles that extend from the midgut region. The vas deferens, which leads posteriorly to the caudal organ complex, appears to have its own distinct circular muscles (not shown). These muscles are very thin circular fibers that are not obviously part of the splanchnic musculature. The caudal organ complex is also muscular. The muscle fibers of CO-R are thick bands arranged in a somewhat unusual spiral-like pattern: dorsally they have a distinctly longitudinal orientation, while ventrally they are oriented transversely (Fig. 3B,C). The distal end of the caudal organ that faces CO-L does not possess any muscles on its ventral side (see arrowhead, Fig. 3C). This is difficult to view in most confocal micrographs without the assistance of 3D rendering software. The left-side caudal organ (CO-L) is wrapped in circular muscles, but these muscles are much thinner and looser in appearance than those of CO-R. The frontal organ does not appear to be muscular, but may be encased under the circular muscles of the midgut (not shown).

Discussion

Oregodasys ashleigha is the second species of Gastrotricha described from the island of Tobago; the first was a marine chaetonotid, Musellifer tridentatus Kånneby, Atherton & Hochberg, 2014, described from Angel Reef at 16 m depth. O. ashleigha is the fourth species of the genus described from the Caribbean: the first two species are O. katharinae Hochberg, 2010 and O. norenburgi Hochberg, 2010 from Carrie Bow Cay, Belize; and the third, O. caymanensis Hochberg, Atherton & Kieneke, 2014 from Little Cayman Island. The Tobagan specimens of Oregodasys were found at 88 m depth in bare sand with other gastrotrichs including species of Chaetonotus, Macrodasvs, Mesodasys, Tetranchyroderma and Urodasys. With a dissection microscope, the species from Tobago can be easily distinguished from other species of Oregodasys by the presence of red ocelli and by its unusual body shape, which is characterized by a large, bilobed or heart-shaped caudal end.

The species from Tobago can be distinguished from other all other species of Oregodasys based on the presence of the large, elliptical red ocelli. Similar red ocelli, but much smaller, are present in only five other species: O. ocellatus, O. norenburgi, O. ruber, O. styliferus, and O. tentaculatus. As previously mentioned, the ocelli of the new species are quite unusual in form. Instead of appearing as relatively spherical bodies containing red pigments as in e.g., O. norenburgi (Hochberg 2010), the ocelli are elongate and somewhat elliptical in shape, 25-32.5 µm long. The new species also differs from other "eyed" species by both the structure of the caudal end and the number and arrangement of adhesive tubes. For example, O. ocellatus differs from O. ashleigha by possessing dorsolateral adhesive tubes, paired pedicles that bear TbP, and by a different number and distribution of TbL (20 in O. ocellatus, 10 in O. ashleigha). Unlike the new species, O. ruber, O. styliferus and O. tentaculatus have paired head appendages and possess a different number and distribution of TbL (absent in O. ruber, 30 in O. styliferus, 75 in O. tentaculatus) and TbA (30 in O. ruber, 30 in O. styliferus, 40 in O. tentaculatus). Oregodasys norenburgi differs from the Tobagan species by possessing short caudal pedicles, having a different number of TbA (32), and a different number and distribution of TbL (19).

Six species of *Oregodasys* possess cirri in a similar location as the new species, but generally in lower numbers: *O. pacificus* has 5 cirri/side; *O. mastigurus* and *O. phacellatus* have 7–10 cirri/side; *O. cayman*ensis and *O. katharinae* have 8 cirri/side; and *O. itoi* has 10 cirri/side. Only *O. cirratus* posseses numerous cirri, but it is worth noting that they form a longitudinal column down the length of the animal rather than being concentrated at the posterior end (Rothe & Schmidt-Rhaesa 2010).

The structure of the male reproductive system of O. ashleigha follows a common pattern in the genus by possessing a right testis with a vas deferens that extends toward the caudal organ complex. The distal portion of the vas deferens appears to be wrapped in a thin layer of circular muscles. The caudal organ complex of the Tobagan species is bipartite in organization (as opposed to a singular organ system) and similar to several other species including: O. caymanensis, O. katharinae, O. maximus, O. mastigurus, O. ocellatus, O. phacellatus, and O. styliferus. These two parts to the caudal organ complex are commonly referred to as penis and bursa (sensu Boaden 1965), with the distinction being that the penis receives the vas deferens, although the exact function of each organ remains to be determined (but see Ruppert (1978) for one functional hypothesis). In O. ashleigha, the CO-R is a distinctly muscular organ with an unusual orientation of muscles that differ between dorsal and ventral sides: the muscle fibers on the dorsal side are oriented longitudinally and those on the ventral side are oriented transversely. Curiously, the muscles do not wrap around the entire organ but instead terminate on the ventral posterior side, leaving a distinct gap where CO-R faces CO-L; this gap does not appear to be an artifact of the staining, and any muscles observed in this region (see Fig. 3D) are extensions of the muscles of CO-L. The CO-L is also covered in muscles, but these muscles are exclusively circular in orientation and loosely arranged around the organ. Other species of Oregodasys are also noted to possess muscles around their caudal organs, but only O. cirratus has had its musculature examined in detail (Rothe & Schmidt-Rhaesa 2010). In this species, only circular muscles are reported, suggesting that both the structure of the caudal organ complex (bipartite vs. solitary) and the orientation of muscles (circular vs. other orientations) may be of taxonomic value.

Acknowledgments

This research is supported in part by Science without Borders/CNPq - Conselho Nacional de Desenvolvimento Cientifico e Tecnologico, Brazil. Collections of specimens for this research were supported by the National Science Foundation to RH (DEB 0918499). Any opinions, findings, and conclusions or recommendations expressed in this material are to be attributed to the authors and do not necessarily reflect the views of the National Science Foundation.

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Associate Editor: Alexander Kieneke